The role of interspecific competition and hybridization in phenotypic evolution of *Passer* sparrows

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ABSTRACT

Interactions between closely related species, including resource competition and hybridization, might influence phenotypic evolution and play a significant role in evolutionary diversification. There may be different outcomes of such interactions on phenotypic evolution. In sympatry, traits may diverge to diminish interspecific competition or maladaptive hybridization, a process known as character displacement, or they may convergence for instance due to gene flow. I studied phenotypic evolution in three taxa of *Passer* sparrows by comparing trait values of several morphological characters (beak height, beak length, tarsus length, wing length and bib size) in sympatric and allopatric populations of the Spanish sparrow (*Passer hispanoliensis*), Italian sparrow (*Passer italiae*) and house sparrow (*Passer domesticus*). The Italian sparrow has a hybrid origin and is intermediate between its two parental species, the house and Spanish sparrow both genetically and phenotypically. I looked for patterns of convergence or divergence in sympatry and inferred these patterns in light of evolutionary processes. I found a complex pattern of sympatric convergence, divergence and parallel shifts in the different traits and species. This complexity may be a result of the interplay between gene flow and divergent and convergent natural selection affecting the traits. However, the Spanish sparrow stood out as one showing more consistent patterns of trait divergence in sympatry with either of the two other species. The Spanish sparrow also appear to occupy a broader niche when in allopatry than in sympatry, suggesting that interspecific competition may have played a significant role in shaping its ecologically relevant traits.

INTRODUCTION

When differentiated but closely related taxa come into contact, they may affect each other's evolutionary trajectories (Brown & Wilson 1956; Grant 1972; Schluter 2000a; Schluter 2000b; Coyne & Orr 2004; Mallet 2007). Due to recent common ancestry, such taxa are likely to be similar in phenotype, both morphologically and behaviorally, increasing the likelihood of interbreeding. Also, closely related taxa are expected to share similar ecologies (Wiens & Graham 2005), leading to competition for essential resources (Cody 1969). These processes, hybridization and ecological competition, will in turn affect the phenotypic evolution of such taxa.

Natural selection may favor character displacement in ecologically important traits that reduce competition between taxa. This process, through which the state of a trait is changed by natural selection as a result of the presence of another ecologically or reproductively similar species (Brown & Wilson 1956; Grant 1972), is thought to be the main evolutionary consequence of resource competition (Fox & Vasseur 2008). Character displacement has been reported across many taxa (Rice & Pfennig 2010) and its role in increasing isolation between taxa is well recognized (Reifová et al. 2011). Examples of such displacement have been found for beak size in Galapagos finches (Lack 1947; Schluter & Grant 1984; Schluter et al. 1985) or body size in island lizards (Schoener 1970; Losos 1990). However, 2008). Haavie et al. (2004) reported that the song of the pied flycatcher (*Ficedula hypoleuca*) has converged towards that of the collared flycatcher (*F. albicollis*) due to heterospecific copying which may facilitate interspecific territoriality. Further, phenotypes may differ between sympatry and allopatry for other reasons than interactions between the species. For example, in sympatry, a species pair may converge phenotypically due to local adaptation to a common habitat that differs from those in allopatric regions. Hall et al. (1966) reported a parallelism on plumage characteristics of pairs of African Bush Shrike species of the genus *Malaconotus*.

In addition to competing, closely related species may exchange genes. Introgressive hybridization and gene flow may result in complete or partial fusion of differentiated lineages so that phenotypic differentiation is reduced and genetic divergence between the populations hindered (Senar et al. 2006, Räsänen & Hendry 2008). On the other hand, if interspecific pairing is maladaptive, e.g. because the resulting hybrids have low viability or fertility, natural selection may favor divergence in traits that reduce interbreeding and increase assortative mating. This may lead to the build-up reproductive isolation through a process known as reinforcement (Servedio & Noor 2003). Reinforcement is the adaptive strengthening of pre-mating barriers between taxa that have already developed some post-mating isolation, and is considered to be an evolutionary response to maladaptive mating behavior (Sætre et al. 1997; Haavie et al. 2004; Price 2008). Finally, hybridization may in some cases lead to the formation of a third, stable hybrid taxon reproductively isolated from either of its parental taxa (Dowling & Secor 1997; Mallet 2007). In this case hybridization does not only favor speciation but possibly also major evolutionary innovations (Servedio & Kirkpatrick 1997; Mallet 2007).

In this thesis, I investigate phenotypic evolution in three taxa of *Passer* sparrows by comparing trait values in sympatric and allopatric populations. The first taxon, the house sparrow (*Passer domesticus*) is a human-commensal sparrow, with a worldwide distribution. Originating in the Middle East, the house sparrow spread through the Paleartic region (*domesticus*-group) and the oriental region (*indicus*-group) following the spread of agriculture some 4000 years ago (Sætre et al., 2012). It occupies a wide range of human-altered habitats including farmlands and cities. Unlike this, the second taxon, the Spanish sparrow (*Passer hispaniolensis*), is usually found in more mesic and moister habitats than the house sparrow, sometimes far from human habitation. Although also the Spanish sparrow feeds off cultivated cereal crops they are not as closely associated with humans as the house sparrow. Its distribution forms a discontinuous belt from the Iberian Peninsula through the Mediterranean region and eastwards to the Middle East and Central Asia. Males of the Spanish sparrow have a black bib much larger than that of the house sparrow spreading out sideways over the breast and extending all along the body flanks (Summers-Smith 1988). The third taxon, the Italian sparrow (*Passer italiae*), is a human-associated, seed-eating bird of hybrid origin, formed by past episodes of interbreeding between the house and Spanish sparrow (Elgvin et al. 2011; Hermansen et al. 2011). It is phenotypically and genetically intermediate between the two parental taxa. Plumage patterns on the head resemble the

Spanish sparrow (chestnut colored head and nape and white cheeks) but the underparts and back resemble the house sparrow (a relatively small black bib that spreads out sideways over the breast, and brown and black streaked back). The Italian sparrow occupies most of the Italian peninsula and some Mediterranean islands and occurs in sympatry with Spanish sparrows in the Gargano peninsula in southeast Italy and with house sparrows in a narrow hybrid zone in the Alps (Summers-Smith 1988; Hermansen et al. 2011). Yet, apparently the parental species can live sympatrically without much hybridization and introgression (J. S. Hermansen, F. Haas, G.-P. Sætre, unpublished data) even though they hybridized in the past to form the Italian sparrow. J. S. Hermansen, F. Haas and G.-P Sætre (unpublished data) found no F1-hybrids in a sympatric population of Spanish and house sparrows in Spain, although backcrossing was detected (house sparrows with introgressed Spanish alleles) indicating asymmetrical introgression. Sympatric Italian and Spanish sparrows on the Gargano peninsula in Southern-Italy do not appear to hybridize at all whereas hybridization occurs between Italian and house sparrows in the Alps (Hermansen et al. 2011). Accordingly, effects of hybridization on phenotypes are likely to be largest in sympatric house and Italian sparrows and smallest in sympatric Italian and Spanish sparrows.

To investigate how species interaction may be affecting phenotypic evolution and speciation, I compared ecologically important traits such as beak length, beak height, wing length and tarsus length as well as one secondary sexual trait, namely bib size, among allopatric and sympatric populations of house, Spanish and Italian sparrows. A unique aspect of my study is that I studied not only the interactions between a hybrid species and its parental species but also between both parental species, which is a unique opportunity to fully investigate the consequences of species interactions at two different phylogenetic levels. Further, it is of particular interest to investigate how phenotypic variation within a hybrid species is affected by species interactions with its parental species. A number of interesting questions can be addressed with the *Passer* sparrow system. For instance, is the covariance structure between traits altered in sympatry and to which extent does this influence divergence and convergence in sympatry? Are the outcomes symmetrical or asymmetrical with respect to which species respond to sympatry and for which types of traits (body size related traits vs. foraging traits (beak) or secondary sexual traits (bib)?

METHODS

Sampling locations and fieldwork

The sampling includes allopatric house sparrows from the northern parts of the Alps in France, Slovenia and Switzerland, allopatric Italian sparrows from the Italian peninsula, allopatric Spanish sparrows from Sardinia, Italian and house sparrows from the contact zone in the Alps, Italian and Spanish sparrows from the contact zone in Gargano and house and Spanish sparrows from the contact zone in western Spain (Fig. 1).

A total of 486 adult male Spanish, house and Italian sparrows were caught using mist nets at 52 localities in five countries (France, Italy, Slovenia, Spain, and Switzerland) during 2007 – 2011. The sample includes 20 allopatric house sparrows (from four localities), 48 allopatric Spanish sparrows (from three localities) and 185 allopatric Italian sparrows (from 22 localities), as well as 50 sympatric Spanish sparrows (36 in sympatry with house sparrows from one locality and 14 in sympatry with Italian sparrow from two localities), 111 sympatric house sparrows (80 in sympatry with Spanish sparrow from one locality and 31 in sympatry with Italian sparrow from nine localities) and finally 72 sympatric Italian sparrows (11 in sympatry with Spanish sparrow from one locality and 61 in sympatry with house sparrows from 13 localities) (see Supplementary Table 1 for detailed localities information).

Each individual was measured after capture for four ecologically important traits: beak height, beak length, tarsus length, and wing length; the first three traits were measured to the nearest 0.1 mm with a dial caliper whereas wing length was measured to the nearest 0.5 mm with a ruler. Finally, the size of a secondary sexual trait, namely the bib, was measured according to a visual scale ranging from 1-5 for house and Italian sparrows and 6-10 for Spanish sparrow.

Permissions for catching and measuring birds were obtained from the appropriate authorities in the respective countries.

Statistical analyses

All calculations were performed using SPSS (version 15, SPSS, Chicago, Ill., USA).

Effects of species interactions on phenotype

I calculated the mean, standard deviation (SD) and coefficient of variation (CV) for each trait across species in sympatry and allopatry to investigate species differences and possible effects of species interactions on phenotypic variation in this system. A coefficient of variation is a normalized measure of relative variation and is used to compare the degree of variation across species and traits. It is expressed as a percentage (%) (CV = 100 * (SD/mean)) (Houle 1992).

I also compared the size ratios of the different morphological traits in allopatry and sympatry and assessed whether any convergence or divergence has occurred in sympatry (Knouft 2003). The size ratio for a given species in sympatry or allopatry was calculated by dividing the largest observed trait value by the smallest trait value. I excluded bib size from the size ratio analysis because of scale incongruence, as bib size was not measured on a metric scale.

I performed General Linear Models (GLM) on all traits studied and all species pairs with two categorical variables as predictors; species and ecology (i.e. allopatry vs. sympatry). I also included the interaction between these two categorical predictors in the model to test whether ecology had a different effect on the respective species. To further distinguish the exact patterns of divergence, convergence or parallel shifts between allopatry and sympatry in each species investigated, I performed Post Hoc Tests (Tukey HDS) between each of the four possible categories investigated.

Effects of species interaction on allometry and phenotypic integration

I performed statistical tests with log-transformed data to assess the allometric relationships among the traits investigated. I used an ANCOVA model on each pair of species to investigate whether allometry of certain characters (namely beak height and length, which relate to the allometric shape of the beak) differed between allopatric and sympatric populations. In the model on log beak length I included one continuous predictor (log beak height) and two categorical predictors (species and ecology) as well as all their possible interactions. If allometry is different in sympatry versus allopatry, it would manifest as a significant interaction between ecology and log beak height. All the non-significant interactions ($P > 0.2$) were removed to improve the fit of the model. I used the same approach to estimate the allometry of overall body shape by investigating size-related traits, namely tarsus length and wing length (Jensen et al., 2003), that is, log wing length with one continuous predictor (log tarsus length) and two categorical predictors (species and ecology) and all their possible interactions.

Finally, to investigate how bib size is integrated (correlated) with other traits and to what extent this trait varies according to the type of species interaction, I estimated a phenotypic integration index based on the average absolute mean values of phenotypic correlation between the bib size and the other traits (Cane 1993; Eroukhmanoff & Svensson 2008). I then compared the percentage of increase (or decrease) of integration between allopatry and sympatry in each species pair comparison.

RESULTS

Associations between species interactions and phenotype

For each trait and in each species in sympatry and in allopatry, the mean size and standard deviation (SD) is presented in Table 1, and the corresponding coefficients of variation (CV) in Table 2. As evident from the two tables, there is considerable size variation within and between species as well as between ecologies (allopatry versus sympatry). The size ratios of four morphological traits in allopatry and sympatry are depicted in Fig. 2. Some traits depart from the null assumption of a 1:1 ratio, showing patterns consistent with convergence or divergence in sympatry (Fig. 2). To further investigate these patterns, I performed GLM analyses on all traits. Below I go through the traits that exhibit significant patterns of convergence, divergence or parallel shifts in sympatry relative to allopatry according to the GLM analyses.

BEAK TRAITS

House sparrows and Spanish sparrows are more different in beak height and beak length in sympatry than in allopatry, consistent with a sympatric divergence in these traits. In particular, the Spanish sparrows have larger beaks in sympatry than house sparrows (Fig 3). This is confirmed by the significant effect of ecology (i.e. sympatry vs. allopatry) in the model (beak length: $F_{1, 173} = 12.055$, $P = 0.001$; beak height: $F_{1, 173} = 12.251$, $P = 0.001$). The two species also differ in beak size in general, as manifested by the effect of species in the model. The Spanish sparrows have larger beaks than the house sparrows (beak length: $F_{1, 173} = 66.727$, $P < 0.001$; beak height: $F_{1, 173} = 3.827$, $P = 0.052$). However, I found no significant ecology x species interaction effect for these two traits (beak length: $F_{2, 172} = 1.698$, $P = 0.194$; beak height $F_{2, 172} = 1.868$, $P = 0.173$), suggesting that sympatry bears the same effects on both species (Fig. 3).

Both the Italian sparrow and the Spanish sparrow have lower beak heights in sympatry than in allopatry (the effect of ecology was significant: $F_{1, 233} = 39.842$, $P < 0.001$). However, I found no significant effect

of either species or ecology x species ($F_{1, 233}$ = 2.277, P = 0.133 and $F_{2, 232}$ = 1.513, P = 0.220 respectively), suggesting that the two species changed in parallel in sympatry (Fig. 3).

Both the house sparrow and the Italian sparrow have shorter beak lengths in sympatry than in allopatry with a significant effect of both ecology and species in the model ($F_{1, 265}$ = 3.977, P = 0.047 and $F_{1, 265}$ = 3.977, P = 0.047 respectively). I found no significant ecology x species interaction for this trait ($F_{2, 264}$ = 0.010, P = 0.922), suggesting again that the two species changed in parallel in sympatry (Fig. 3).

None of the other beak trait comparisons exhibited any significant effects of ecology, species or ecology x species interaction in the GLM analyses (see also Table 1).

SIZE TRAITS

The wing-lengths of Italian and Spanish sparrows tend to be more similar in sympatry than in allopatry, consistent with a pattern of convergence (in allopatry: Tukey post-hoc test: P = 0.001; in sympatry: Tukey post-hoc test: P = 0.991) (Fig 4). The two species had a tendency to change in opposite directions from allopatry to sympatry to converge to a similar value, that is, there was an almost significant ecology x species interaction effect ($F_{2, 231}$ = 3.283, P = 0.071). Yet, there was no significant effect of either ecology ($F_{1, 232}$ = 0.268, P = 0.605) or species ($F_{1, 232}$ = 1.623, P = 0.204) (Fig. 4).

In contrast, Italian and house sparrows have more divergent wing lengths in sympatry than in allopatry, (significant effect of ecology: $F_{1, 266}$ = 13.796, P < 0.001) suggesting a pattern of sympatric divergence. As a result, Italian sparrows have longer wings in sympatry (Tukey post-hoc test: P = 0.001) as manifested by the significant effect of species in the model ($F_{1, 266}$ = 11.839, P = 0.001) (Fig. 4). However, I found no significant interaction effect of ecology x species ($F_{2, 265}$ = 0.026, P = 0.874) (Fig. 4).

Finally, both house and Spanish sparrows tend to have longer tarsi in sympatry than in allopatry as there was a significant effect of ecology ($F_{1, 173} = 10.070$, $P = 0.002$) and in general, the Spanish sparrows have longer tarsi than the house sparrows (there was a significant effect of species: $F_{1, 173} = 21.156$, $P < 0.001$) (Fig. 4). I found no significant interaction effect of ecology x species ($F_{2, 172} = 0.030$, $P = 0.864$) (Fig. 4).

None of the other size trait comparisons exhibited any significant effects of ecology, species or ecology x species interaction in the GLM analyses (see also Table 1).

BIB SIZE

The bib sizes of Italian and house sparrows are consistent with a pattern of a sympatric convergence, because house sparrows have larger bibs in sympatry than in allopatry (Tukey post-hoc test: $P = 0.045$) as there was a significant effect of ecology x species interaction ($F_{1, 291} = 6.793$, $P = 0.010$) (Fig. 5). There was also a significant effect of ecology ($F_{2, 290} = 4.208$, $P = 0.041$), but no significant effect of species ($F_{1, 291} = 0.637$, $P = 0.425$) (Fig. 5).

Similarly, where house and Spanish sparrows are in sympatry, Spanish sparrows show a pattern consistent with convergence towards a smaller bib (Tukey post-hoc test: $P = 0.005$) (Fig. 5). There was a significant effect of both ecology x species ($F_{2, 178} = 12.080$, $P = 0.001$) and species ($F_{1, 179} = 1893.333$, $P < 0.001$), but no significant effect of ecology ($F_{1, 179} = 1.002$, $P = 0.318$) (Fig. 5).

None of the other bib size comparisons exhibited any significant effects of ecology, species or ecology x species interaction in the GLM analyses (see also Table 1).

Effects of species interaction on allometry and phenotypic integration

BEAK SHAPE

I found that beak allometry differed between sympatric and allopatric populations of both the Spanish and the house sparrow, as manifested by a significant interaction of ecology x log beak height ($F_{2, 166} = 4.336$, $P = 0.039$). There was an almost significant effect of log beak height on the model ($F_{1, 167} = 3.773$, $P = 0.054$), suggesting a general allometric relationship between beak dimensions and a significant effect of species, ecology, and species x ecology ($F_{1, 167} = 3.941$, $P=0.049$; $F_{1, 167} = 4.424$ $P = 0.037$; $F_{2, 166} = 3.885$, $P = 0.05$ respectively) (Fig. 6).

Also in the comparison of Italian and Spanish sparrows, I found a difference in beak allometry between allopatric and sympatric populations of the two species, as evidenced by a significant interaction of ecology x log beak height ($F_{2, 198} = 7.274$, $P = 0.008$). There was also an almost significant effect of log beak height on the model ($F_{1, 199} = 3.611$, $P=0.059$), again suggesting that beak dimensions vary allometrically, and a significant effect of ecology ($F_{1, 199} = 6.920$, $P = 0.009$), but no significant effect of species ($F_{1, 199} = 0.020$, $P = 0.888$) (Fig. 7).

None of the other beak shape comparisons exhibited any significant effects of log beak height, species, ecology, ecology x log beak height or species x ecology interactions in the ANCOVA analyses.

SIZE-RELATED TRAITS

I found a significant difference in the allometric relationship between wing length and tarsus length in populations of Spanish sparrows in allopatry and sympatry with house sparrows (significant interaction of ecology x log tarsus length: $F_{2, 163} = 4.422$, $P = 0.037$). I found a significant effect of log tarsus length ($F_{1, 164} = 8.334$, $P = 0.004$), confirming a strong allometric relationship of size-related traits, and of species x ecology ($F_{2, 163} = 4.674$, $P = 0.032$) and ecology ($F_{1, 164} = 4.475$, $P = 0.036$) (Fig. 8).

On the contrary, the allometric relationship between wing length and tarsus length is significant (log tarsus length: $F_{1, 199} = 13.045$, $P < 0.001$) but remains similar between allopatric and sympatric populations of Italian and Spanish sparrows (there was no significant effect of ecology x log tarsus: $F_{2, 198} = 0.181$, P=0.671). There was also no effect of ecology ($F_{1, 199} = 0.172$, P = 0.679). However, there was a significant effect of species ($F_{1, 199} = 7.493$, P=0.007), and species x log tarsus length ($F_{2, 198} = 7.185$, P = 0.008) (Fig. 9).

None of the other size trait comparisons exhibited any significant effects of log tarsus length, species, ecology, ecology x log tarsus length or species x ecology interactions in the ANCOVA analyses.

I further estimated how bib size is integrated (correlated) with other traits. Where Italian and Spanish sparrows are in sympatry there is a pattern such that when one trait (beak height, beak length, tarsus length, wing length) is positively correlated with bib size in one species, it is negatively correlated in the other species and vice versa. However, this seems not to be the case in allopatry (Table 3). None of the other species pair interactions exhibit the same pattern.

Finally, I estimated the percentage of increase of bib integration between allopatry and sympatry across species. Where the house sparrow is in sympatry with the Italian sparrow there is an increase in bib integration relative to allopatry (100%), but not where it is in sympatry with the Spanish sparrow (0%). There is an increase of bib integration in the Italian sparrow where they are in sympatry with the two putative parental species (16.7% in sympatry with the house sparrows and 333.3% in sympatry with the Spanish sparrows). There is also an increase in bib integration in the Spanish sparrow where they are in sympatry with both house (8.3%) and Italian sparrows (266.7%) (Fig. 10).

DISCUSSION

I compared phenotypic traits among allopatric and sympatric populations of the three sparrow species Italian, Spanish and house sparrow, to look for patterns such as convergence, divergence and parallel shifts. I found some overall differences between the species. For instance, comparing allopatric populations, Spanish sparrows have larger beaks, longer tarsi and wings and larger bibs than allopatric house sparrows. The hybrid Italian sparrow is intermediate to the parental species in most traits but has for instance longer wings than either of them. Importantly, however, I found a variety of differences in traits values, and in the way they integrate with each other, between allopatry and sympatry suggesting that species interactions may have influenced phenotypic evolution in the sparrows in complex ways. These patterns also tended to be asymmetric in certain combinations of traits and species interactions, meaning shifts mostly or only occurred in one taxon. Below I go through how each of the traits differ between sympatric and allopatric species pairs and try to infer how processes such as competition, hybridization and local adaptations may have affected phenotypic evolution.

Changes in beak dimensions and shape

Comparing beak morphology in allopatric and sympatric species pairs, I found different patterns of divergence due to sympatry. In Spanish sparrows and house sparrows, I found evidence for sympatric divergence in beak size. This was mainly caused by Spanish sparrows having larger beaks (both higher and longer) in sympatry with the house sparrow than in allopatry. Allopatric Spanish sparrows do have larger beaks than allopatric house sparrows. Hence, the pattern in sympatry apparently represents an accentuation of existing species difference. This pattern is consistent with ecological character displacement (Grant 1972). Competition for food may have affected the Spanish sparrow in such a way that it has specialized on larger and/or harder seeds when in sympatry with the house sparrow compared to the allopatric situation. In contrast, I found no evidence of character displacement where the Italian sparrow interacts with either of its parental species. The Italian and Spanish sparrow both had lower beak heights in sympatry compared to in allopatry and the Italian and house sparrow both

had shorter beak lengths in sympatry than in allopatry. This rather reflects a possible case of local adaptation to an exogenous selective pressure (for instance seed size and food availability in general which might differ in these sympatric regions, especially in the Alps). The beak has an important function in feeding in birds. Eroukhmanoff et al. (2012) found that beak morphology within the Italian sparrow is influenced by climatic factors. Indeed, climatic factors have an impact on local agricultural practices and on the availability of food resources, and hence are likely to affect the local optimum of size and shape of beak (Symonds & Tattershall 2010; Schluter & Grant 1984). Tentatively, I suggest that a combination of interspecific competition and local adaptation to prevailing ecological conditions could explain the discrepancies between the patterns found in the different species pairs.

Interestingly, I also found that beak shape, and more specifically the allometric relationship of the beak dimensions, has been altered in some sympatric situations irrespective of whether the traits themselves were displaced or not. Indeed, in the sympatric situations where Spanish sparrows were in contact with either house or Italian sparrows, not only did the shape of the beak change, but there was no longer any significant allometric relationship between beak height and length in this species. Beak allometry has been widely studied, and is known to be controlled by few genes during embryonic development (Abzhanov et al. 2004, Mallarino et al. 2011). In many cases of bird adaptive radiations such as the Galapagos finches and the Hawaiian Honeycreepers (Lack 1947, Lovette et al. 2002), ecological displacement has been shown to occur on the shape rather than the dimensions of the beak, and as a response to different ecological niches and seed availabilities. Thus, these findings might reflect the consequences of competition for food in sympatric situations, which were not detected at the univariate level (such as in the interaction between Italian and Spanish sparrows, where only the beak allometry of Spanish sparrows seems to have been displaced). Furthermore, the loss of an allometric relationship (phenotypic integration) in sympatry in Spanish sparrows implies a change in the fitness landscape that reduces phenotypic or genetic correlations between beak traits. Such a change would alter the potential evolutionary trajectory of these two traits by reducing constraints on independent adaptive evolution (Schluter 1996). Further analysis, for instance using geometric morphometrics, is needed to assess the extent of these changes in beak shape.

Changes in body size and shape

Body size is a main factor in niche differentiation among closely related species (Wilson 1975). When body size changes as a response to different environmental conditions one also expects changes in other features of an organism (Knouft 2003). Hence, understanding the implications of body size evolution is crucial for understanding the evolution of an array of morphological and physiological traits (Futuyma 2009).

Wing length can constitute a good approximation of body size in birds (Grant 1972, Gosler et al. 1998). I found that this trait either converged or diverged depending on the different sympatric situations studied here. I found that the Italian sparrow diverged towards longer wings when in sympatry with the house sparrow, possibly reflecting ecological character displacement. Wing length might be of importance for dispersal and migration processes, as well as for foraging or escaping predation. Without additional data on wing length, it is however impossible to formulate a reasonable explanation for this pattern. In general, the Italian sparrow is phenotypically intermediate to the parental species, except for wing length, in which it has the highest trait values. However, when the Italian sparrow is in sympatry with the Spanish sparrow, the Spanish sparrow converged in a tendency of having longer wings. Tarsus length may also reflect body size in birds. When I compared the parental species in allopatry and sympatry, I found a pattern of parallel shift with a tendency towards longer tarsi in both species when in sympatry. Parallel shifts such as these suggest convergence due to shared ecological conditions rather than interactions between the sparrow species. However, other sympatric situations did not seem to lead to any particular changes in tarsus length.

Allometric relationships related to body size are generally the consequences of adaptation (Futuyma 2009) and tend to be strongly conserved across closely related taxa (Klingenberg 2008, Klingenberg and Zimmermann 1992). It is surprising therefore that when the Spanish sparrow is in sympatry with the house sparrow, there is a clear shift in the allometric relationship between tarsus and wing length (the relationship even becomes negative). This however does not seem to be the case when other species interact (even when Spanish and Italian sparrows are in sympatry), which is more in line with

expectations. This extensive change in overall body shape of the Spanish sparrow, i.e. Spanish sparrows having shorter wings when tarsus length increases, and hence a more robust shape, is intriguing. This pattern may of course result from sympatric Spanish sparrows being migratory as opposed to the allopatric Spanish sparrows, which have more of a nomadic behavior. Nevertheless, I am not aware of many studies reporting such a clear shift in body shape at the intraspecific level, whether it is due to interspecific competition or migration adaptation.

Changes in a secondary sexual trait and its integration

Male bib size in sparrows is a signal involved in female mate choice, as well as an important factor in social behavior (Møller 1989; 1990; Kimball 1996; Nakagawa et al. 2007; Griggio & Hoi 2010). Hence it has the potential to promote reproductive isolation. Bib size converged in two out of the three possible species interactions. More precisely, the Spanish sparrow converged towards a smaller bib size when in sympatry with the house sparrow, and the house sparrow converged towards a bigger bib size when sympatric with the Italian sparrow. It is interesting to see that in two out of the three possible interactions, there was such convergence, which might indicate some degree of gene flow between the species, as should be expected in the Alps at least (Hermansen et al. 2011). However, trait convergence in bib size in Spain may be an artefact of Spanish males not beeing in breeding mode yet (F. Haas personal communication). Secondary sexual traits can play a vital role in species recognition and reproductive isolation (Svensson et al. 2007). Thus the apparent absence of reproductive character displacement in our system, and even more so, the convergence of this secondary sexual trait in two of the three sympatric situations, is puzzling, particularly alongside divergence in other traits. Of course, behavior and especially song might play a more efficient role in isolating these species. But it has also been shown that species recognition does not necessarily rely only on one single trait but a combination of sexual and non-sexual traits, and their association might be reinforced in the face of gene flow (Merril et al. 2010). Interestingly, I found that the bib integrated to other non-sexual traits considerably more in sympatry in all sympatric situations for at least one species. Moreover, when Italian and Spanish sparrows were in sympatry, the phenotypic correlations between bib size and other traits were consistently of opposite signs across species, although overall bib size was not altered. These two

findings may suggest that the overall phenotypic integration of the bib tends to be displaced in sympatry, possibly to facilitate species recognition.

CONCLUSIONS

None of the three species show the same pattern of sympatric trait change and thus I found little consistency in the outcomes of interacting with one or the other species. However, the Spanish sparrow is the species that show more morphological shifts when it is in sympatry with the other two species. As mentioned before, the Spanish sparrow is less human-associated than the house sparrow. In the allopatric Sardinian populations, however, Spanish sparrows seem to have a broader niche (TO Elgvin, JS Hermansen, SA Sæther & G-P Sætre personal observations). Whereas Spanish sparrows are absent from towns and cities in Spain and in the Gargano peninsula, a niche instead occupied by house sparrows, they are abundant in Cagliari and other towns in Sardinia. When a species is freed from interspecific competition its niche is likely to expand and this will affect the mean and variance of ecologically relevant traits. This process is known as character release and is the antithesis of character displacement (Grant 1972). The change in allometry of the beak of Spanish sparrows in sympatry with both the house and Italian sparrow relative to the allopatric Sardinian populations points to a common cause, and that cause may simply be presence/absence of a closely related food competitor. It is tempting to speculate that absence of competition in Sardinia may also explain the other trait changes in the Spanish sparrow. As discussed above the sympatric shift in body shape and wing length of Spanish sparrows, particularly in sympatry with the house sparrow, could be due to differences in migration behaviour. It is possible that Sardinian Spanish sparrows have abandoned winter migration because the human commensal niche becomes available when house or Italian sparrows are absent. Humans provide year-round supply of sparrow food through storage of cereals, spilling and feeding of domestic animals and hence, there is no need to migrate south during winter. As a parallel, the only non-commensal house sparrow, the sub-species *P. d. bactrianus*, is also the only subspecies that migrates south during winter (Sætre et al. 2012). The latter authors suggested that the sedentary behaviour of commensal house sparrows indeed may be an adaptation to human commensalism.

Finally, it is perhaps not so surprising that the pattern of character changes in sympatry is so complex across the three species. In addition to compete for resources they also hybridize to variable extents

(Hermansen et al. 2011). Hybridization and competition may affect the various phenotypic traits differently. Ecologically important characters may diverge despite hybridization, whereas neutral characters converge because of introgressive hybridization. Similar patterns have been found in the genomes of hybridizing taxa (Turner et al. 2005, Harr 2006, Feder & Nosil 2010). That is, massive introgression can be observed across the genome with the exception of so-called genomic islands of divergence maintained by natural selection and hitchhiking. In a future study it would be interesting to investigate whether such genomic islands of divergence are found in the sparrows and whether the genes involved affect the phenotypic traits that I have found to diverge in sympatry.

Parallel evolution without convergence implies concordant adaptive evolution in the sympatric species pair towards the same ecological niche, and does not suggest any interactions, either competition or hybridization, between the sparrow species. Character displacement implies divergent selection due to ecological competition or to the production of unfit hybrids. Finally, convergence suggests either that competition has led to niches becoming more similar, or that hybridization and introgression have reduced the differences between the taxa that are present in allopatry. All these patterns are found in these sparrow species pairs, suggesting a complex response to competition, hybridization and local ecology. However, the possibility that all the patterns I found are in fact caused by independent responses of the two species to local ecological conditions – with no effect of interactions between species – cannot be ruled out. More studies with greater replication of sympatry and allopatry for all species pairs, and across a variety of environments, are therefore required in order to affirm the impact of species interactions.

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TABLES

Table 1. Mean size and standard deviation for each trait and each species according to ecology (allopatry vs. sympatry). All trait measures are in mm, except bib size where a visual score ranging from 1-10 was used.

		TRAITS														
		Beak Height			Beak Length			Wing Length			Tarsus Length			Bib Size		
SPECIES	ECOLOGY[1]	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N
House	Sympatric (I)	7.59	0.29	46	9.46	0.59	46	78.97	2.39	47	17.21	0.82	47	2.45	0.72	31
Italian	Sympatric (H)	7.69	0.29	101	9.67	0.58	101	79.23	2.69	103	19.12	0.72	103	2.32	0.70	60
House	Sympatric (S)	7.78	0.30	130	9.76	0.60	130	78.17	3.35	130	19.33	0.60	130	2.28	0.93	76
Spanish	Sympatric (H)	8.23	0.33	67	10.1	0.41	67	77.95	2.59	66	19.79	0.65	67	7.56	0.80	36
Italian	Sympatric (S)	7.41	0.34	15	9.27	0.33	15	78.67	1.78	15	19.23	0.67	15	2.45	0.61	11
Spanish	Sympatric (I)	7.45	0.69	14	9.64	0.87	14	79.61	1.15	14	19.55	0.44	14	8.00	0.79	13
House	Allopatric	7.56	0.30	38	9.63	0.53	38	77.50	1.85	38	19.09	0.53	38	1.91	0.57	17
Italian	Allopatric	7.78	0.32	284	9.95	0.84	284	78.57	2.38	283	19.09	0.75	283	2.26	0.66	181
Spanish	Allopatric	8.01	0.23	79	9.82	0.41	79	77.49	2.17	79	19.41	0.53	79	8.15	0.60	48

[1]I = sympatric with Italian; H = sympatric with house; S = sympatric with Spanish sparrows.

Table 2. Coefficient of Variation (CV) in percentage % for each trait and each species according to ecology (allopatry vs. sympatry).

			TRAITS				
REGION	SPECIES	ECOLOGY	Beak Height	Beak Length	Wing Length	Tarsus Length	Bib Size
	House	Sympatric	3.82	6.20	3.03	4.77	29.51
Northern Contact Zone	Italian	Sympatric	3.77	6.01	3.40	3.74	29.96
	House	Sympatric	3.92	6.16	4.29	3.09	40.75
Spain	Spanish	Sympatric	4.06	4.07	3.32	3.27	10.58
	Italian	Sympatric	4.59	3.61	2.26	3.49	24.94
Gargano	Spanish	Sympatric	9.32	9.00	1.44	2.23	9.89
Alps	House	Allopatric	4.02	5.53	2.39	2.78	29.63
Central Italy	Italian	Allopatric	4.15	8.47	3.02	3.92	29.20
Sardinia	Spanish	Allopatric	2.91	4.14	2.80	2.71	7.37

Table 3. Phenotypic correlation between bib size with other traits in sympatry and allopatry of Italian and Spanish sparrows.

ECOLOGY	TRAITS	SPECIES	
		Spanish	Italian
Allopatry	Beak Height	-0.124	-0.096
	Beak Length	-0.028	-0.118
	Wing Length	-0.076	-0.022
	Tarsus Length	0.250	0.012
Sympatry	Beak Height	-0.588	0.134
	Beak Length	-0.445	0.090
	Wing Length	0.471	-0.492
	Tarsus Length	0.271	-0.318

FIGURES

Figure 1. Distribution map of the species complex. Distribution of the house sparrow (grey area), Spanish sparrow (red area) and Italian Sparrow (yellow area). Hatched grey/red areas indicates zones of distributional overlap between house and Spanish sparrows. A narrow contac zone between house and Italian sparrows in the Alps is indicated with grey/yellow colour.

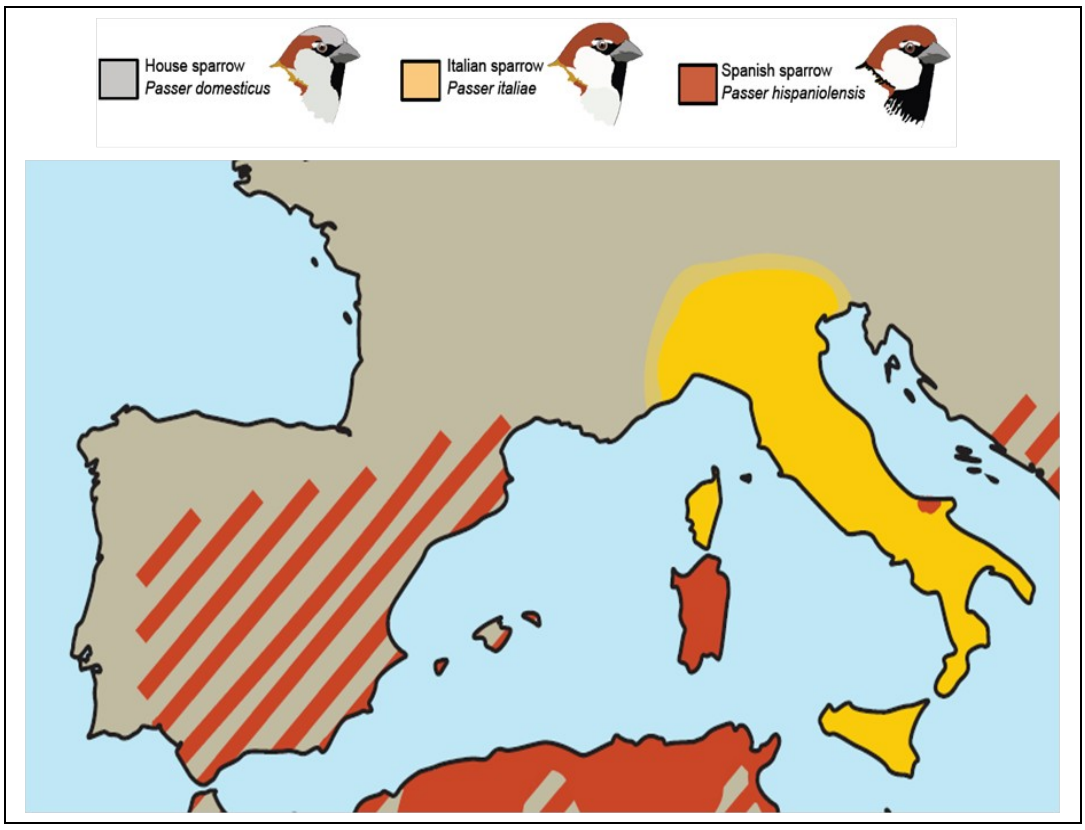


Figure 2. Size ratios (the largest observed trait value divided by the smallest trait value for a given species in sympatry or allopatry) of four morphological traits in allopatric and sympatric populations of the house sparrow, Italian sparrow and Spanish sparrow. If size ratios of a sympatric species pair is larger than ratios generated from allopatric populations this indicates possible divergence, if it is smaller this indicates possible convergence. ◊ = beak length, □ = beak height, O = tarsus length and Δ = wing length.

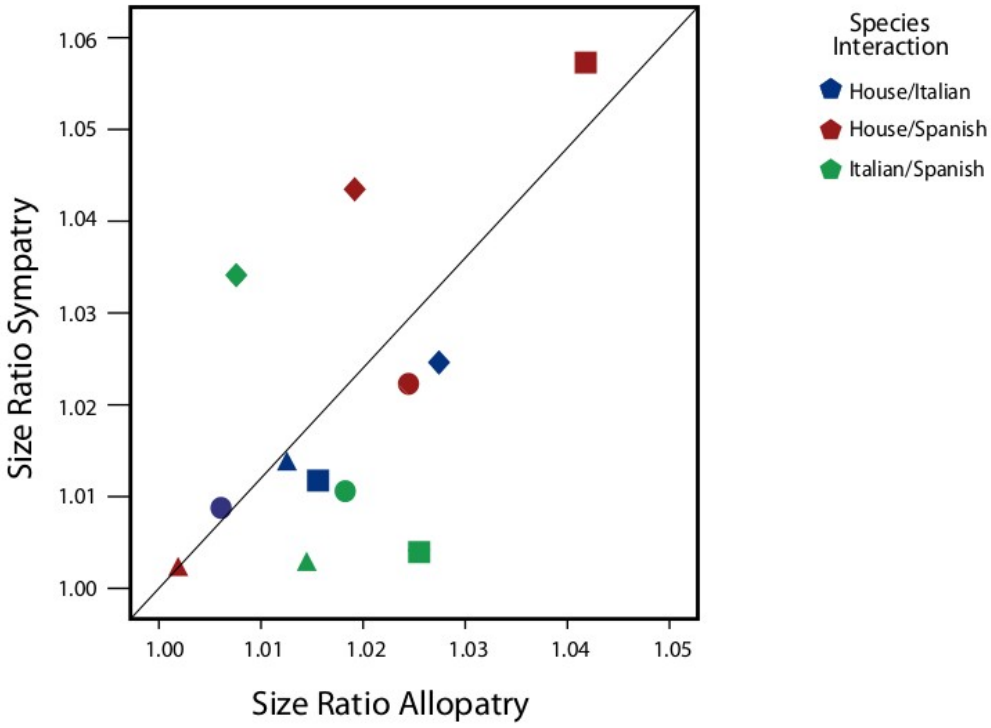


Figure 3. Mean (± SD) beak sizes (mm) of sympatric (center) and allopatric (periphery) populations of three species of sparrows. Bars not sharing a letter differ significantly at P = 0.05 according to a Tukey post-hoc test. (Top left) beak heights of house and Spanish sparrows; (top right) beak heights of Italian and Spanish sparrows; (bottom left) beak length of house and Spanish sparrows; (bottom right) beak length of house and Italian sparrows.

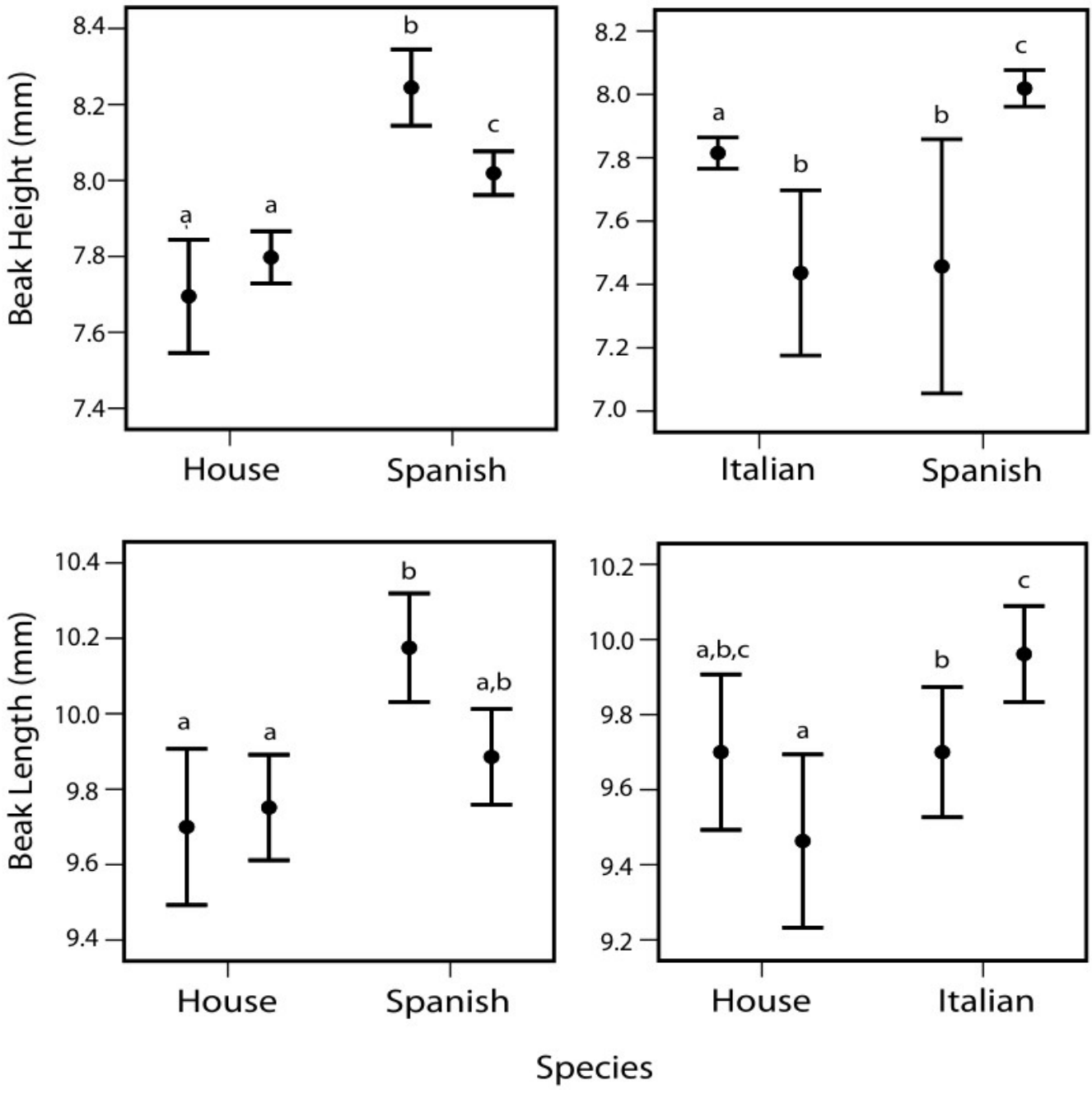


Figure 4. Mean (± SD) wing and tarsus lengths (mm) of sympatric (center) and allopatric (periphery) populations of three species of sparrows. Bars not sharing a letter differ significantly at P = 0.05 according to a Tukey post-hoc test. (Top) wing length of Italian and Spanish sparrows; (centre) wing length of house and Italian sparrows; (bottom) tarsus length of house and Spanish sparrows.

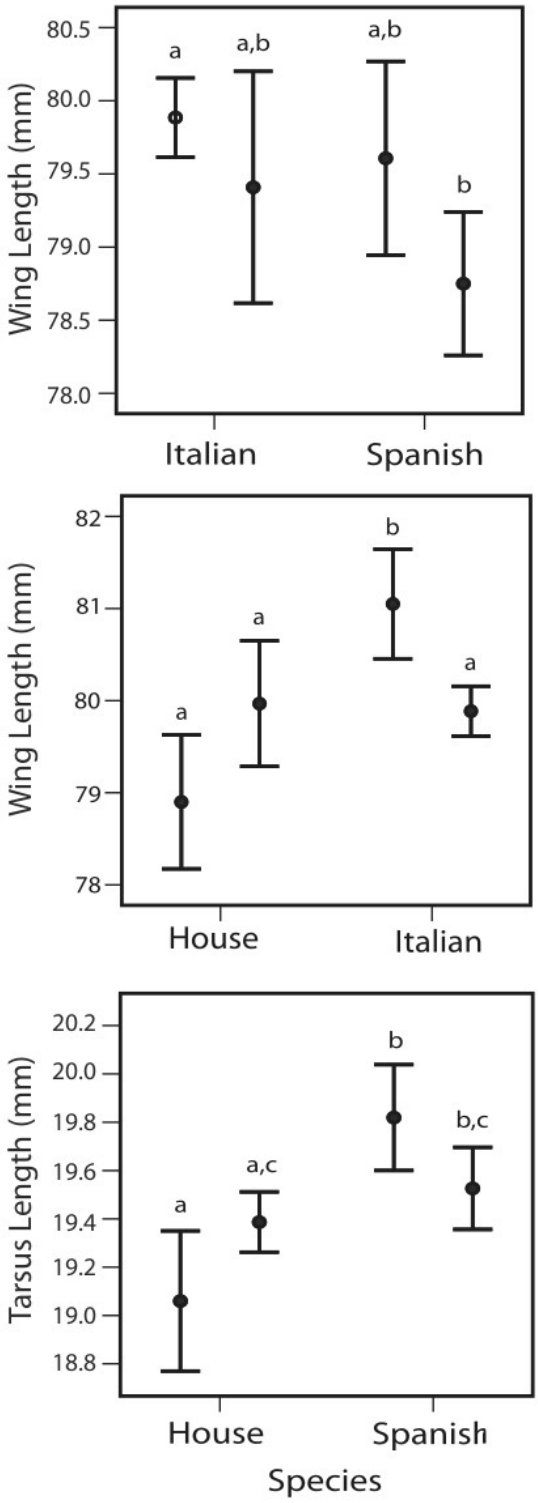


Figure 5. Mean (± SD) bib size according to a scale ranging from 1-10 of sympatric (center) and allopatric (periphery) populations of three species of sparrows. Bars not sharing a letter differ significantly at P = 0.05 according to a Tukey post-hoc test. (Left panel) bib size of house and Italian sparrows; (right panel) bib size of house and Spanish sparrows.

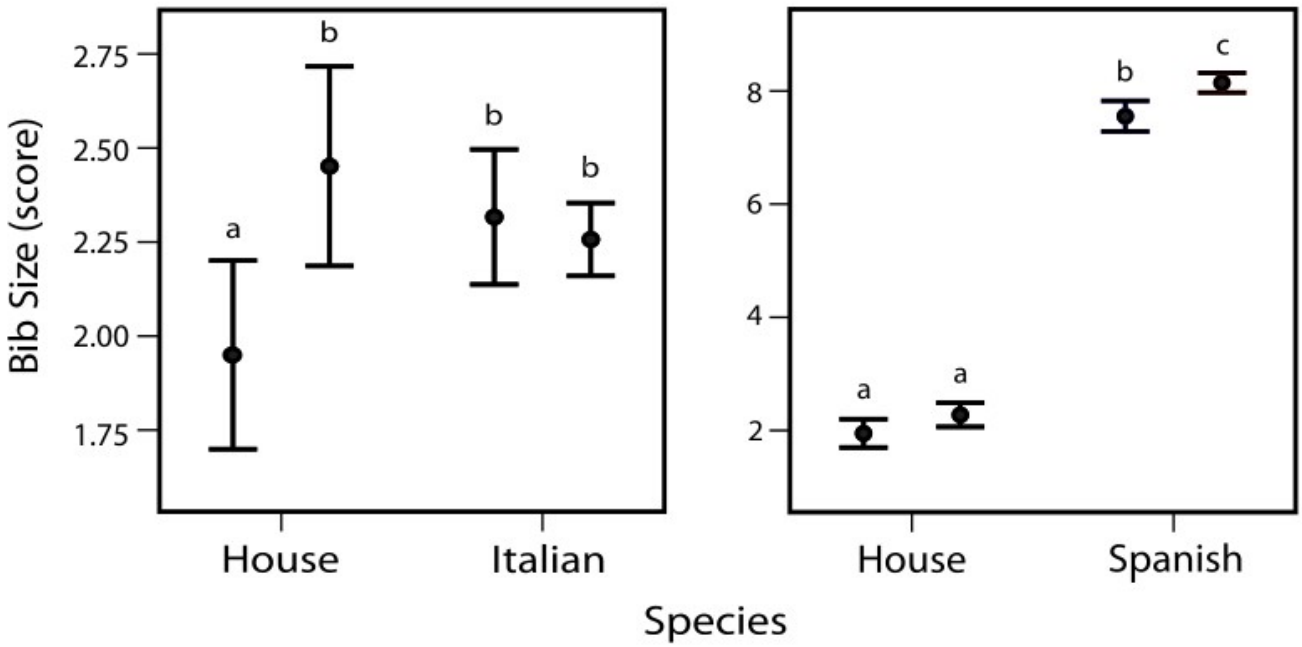


Figure 6. Allometric relationship of beak length (mm) and beak height (mm) in allopatric (blue) and sympatric (green) house (left panel) and Spanish sparrows (right panel). Regression lines: allopatric house sparrow $R^2 = 0.113$; sympatric house sparrow $R^2 = 0.058$; allopatric Spanish sparrow $R^2 = 0.212$; sympatric Spanish sparrow $R^2 = 0.013$.

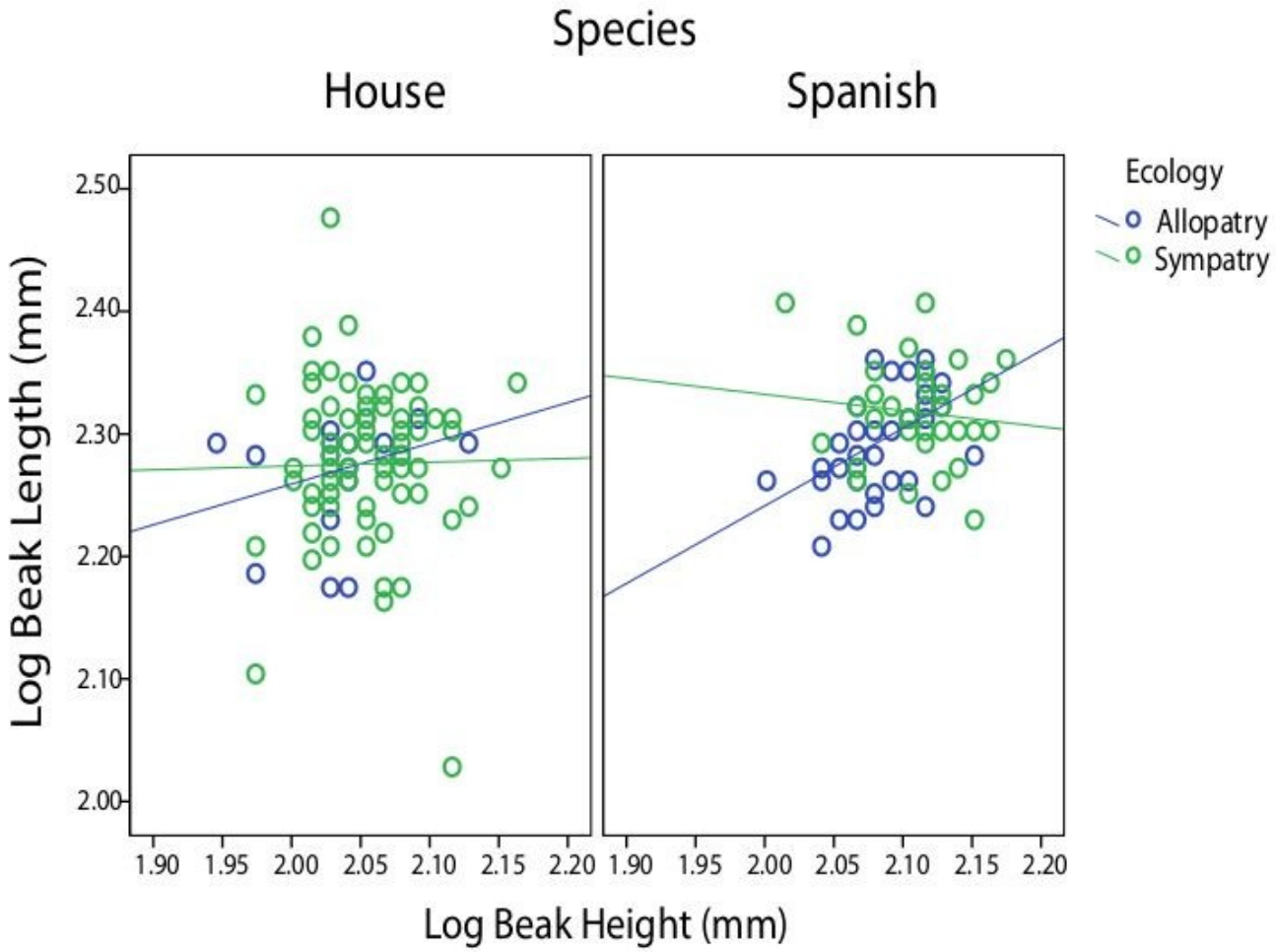


Figure 7. Allometric relationship of beak length (mm) and beak height (mm) in allopatric (blue) and sympatric (green) Italian (left panel) and Spanish sparrows (right panel). Regression lines: allopatric Italian sparrow $R^2 = 0.150$; sympatric Italian sparrow $R^2 = 0.121$; allopatric Spanish sparrow $R^2 = 0.231$; sympatric Spanish sparrow $R^2 = 0.009$.

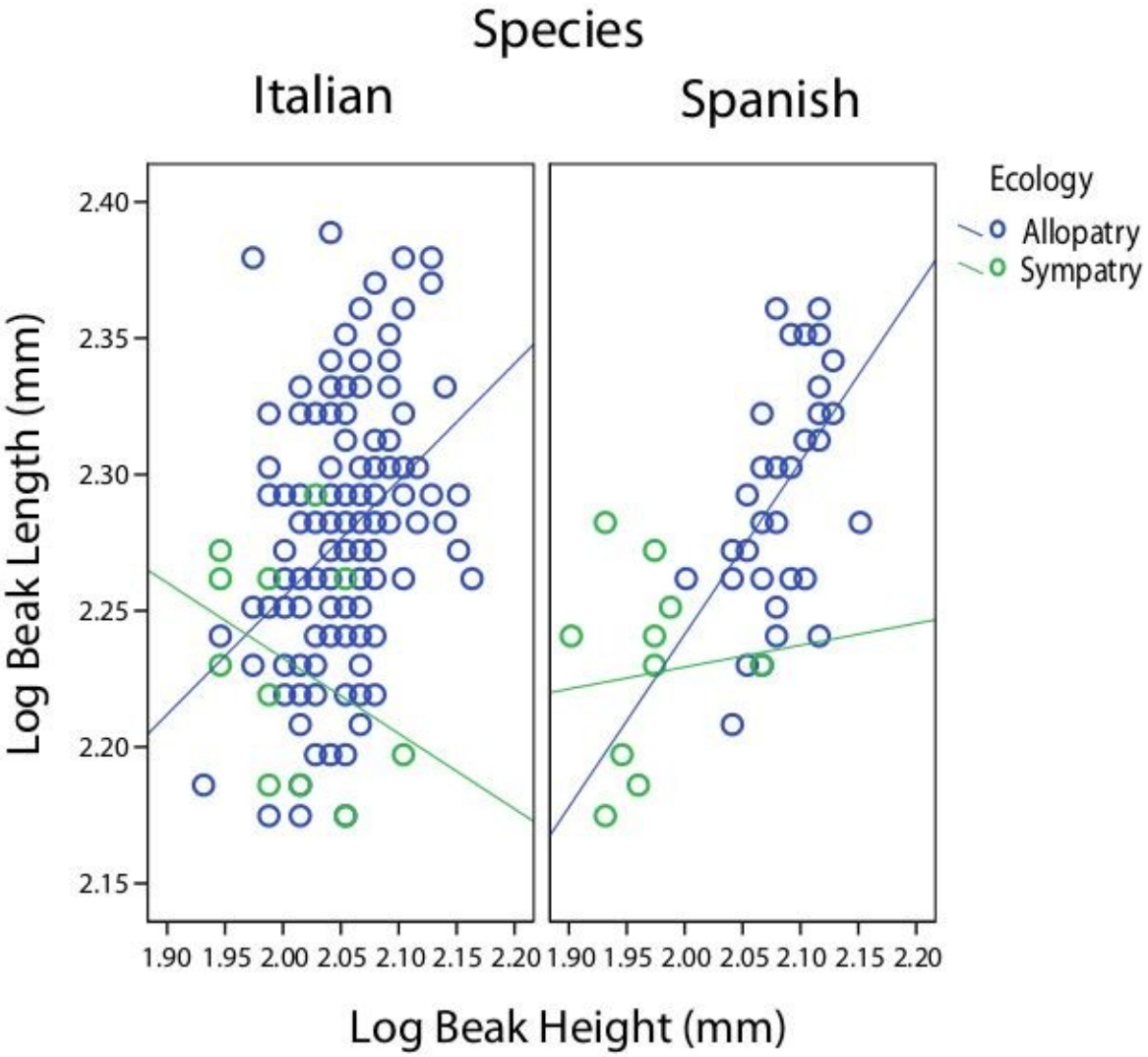


Figure 8. Allometric relationship of wing length (mm) and tarsus length (mm) in allopatric (blue) and sympatric (green) house (left panel) and Spanish sparrows (right panel). Regression lines:allopatric house sparrow $R^2 = 0.113$; sympatric house sparrow $R^2 = 0.058$; allopatric Spanish sparrow $R^2 = 0.212$; sympatric Spanish sparrow $R^2 = 0.013$.

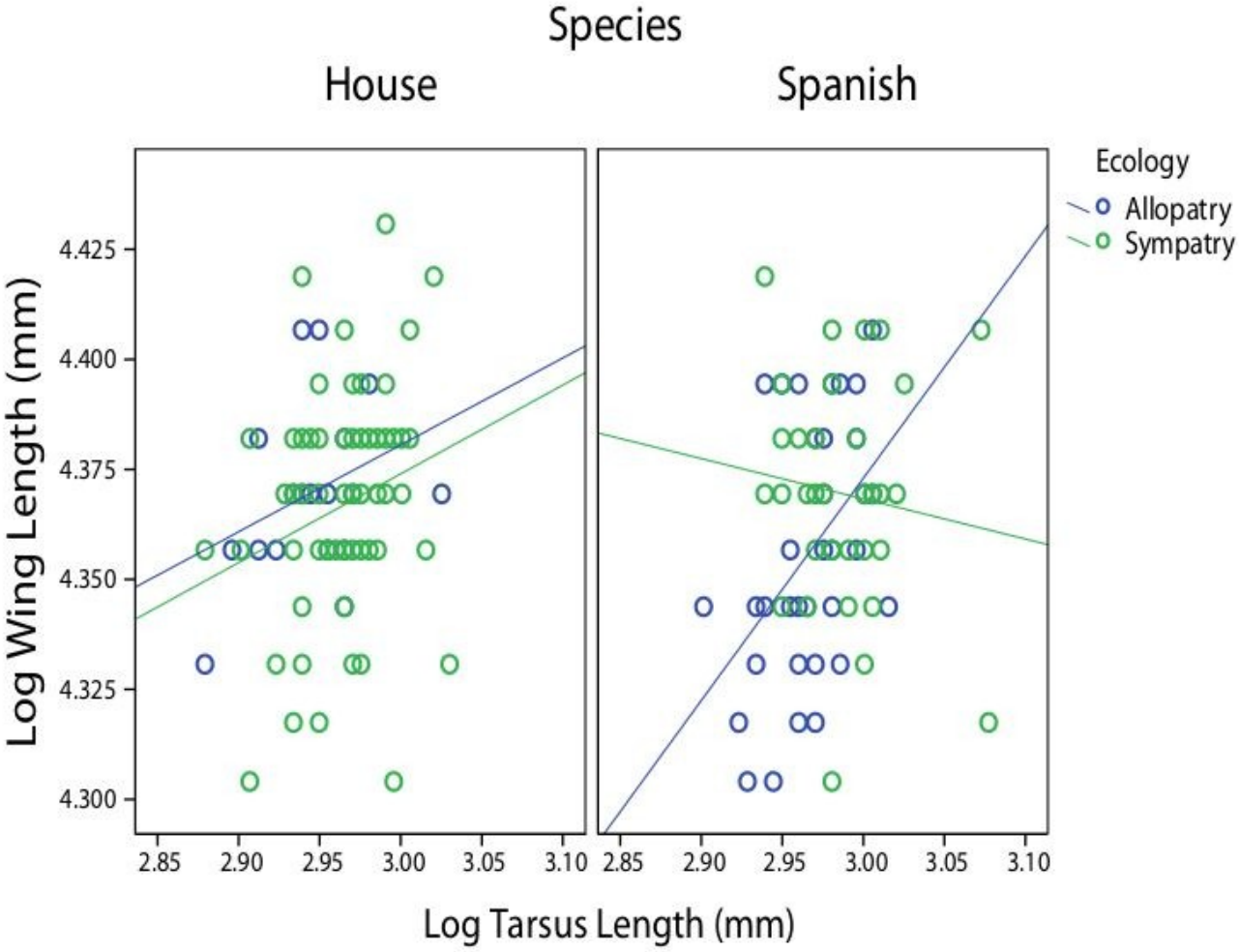


Figure 9. Allometric relationship of wing length (mm) and tarsus length (mm) in allopatric (blue) and sympatric (green) Italian (left panel) and Spanish sparrows (right panel). Regression lines: allopatric Italian sparrow $R^2 = 0.034$; sympatric Italian sparrow $R^2 = 0.259$;allopatric Spanish sparrow $R^2 = 0.212$; sympatric Spanish sparrow $R^2 = 0.087$.

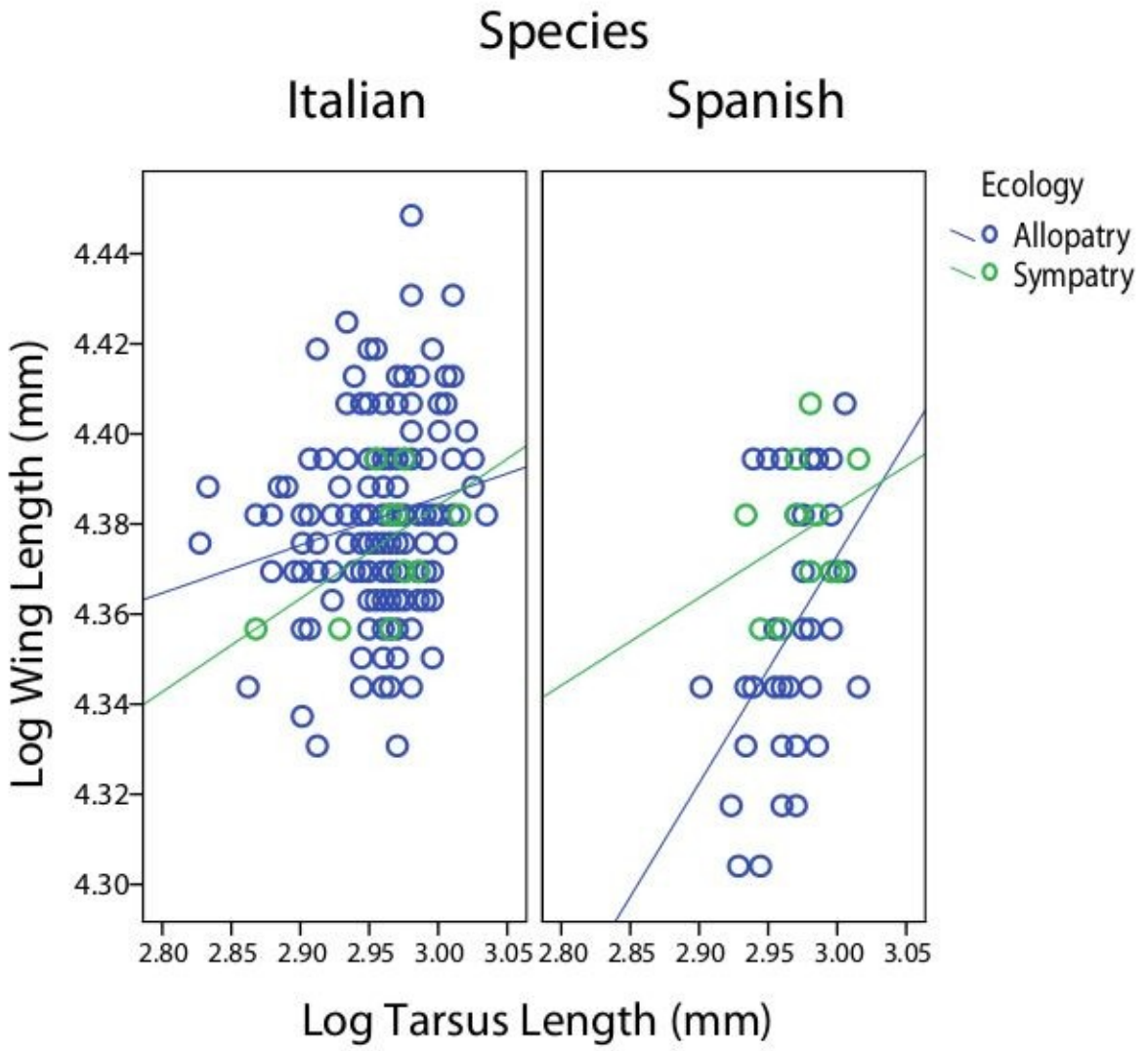
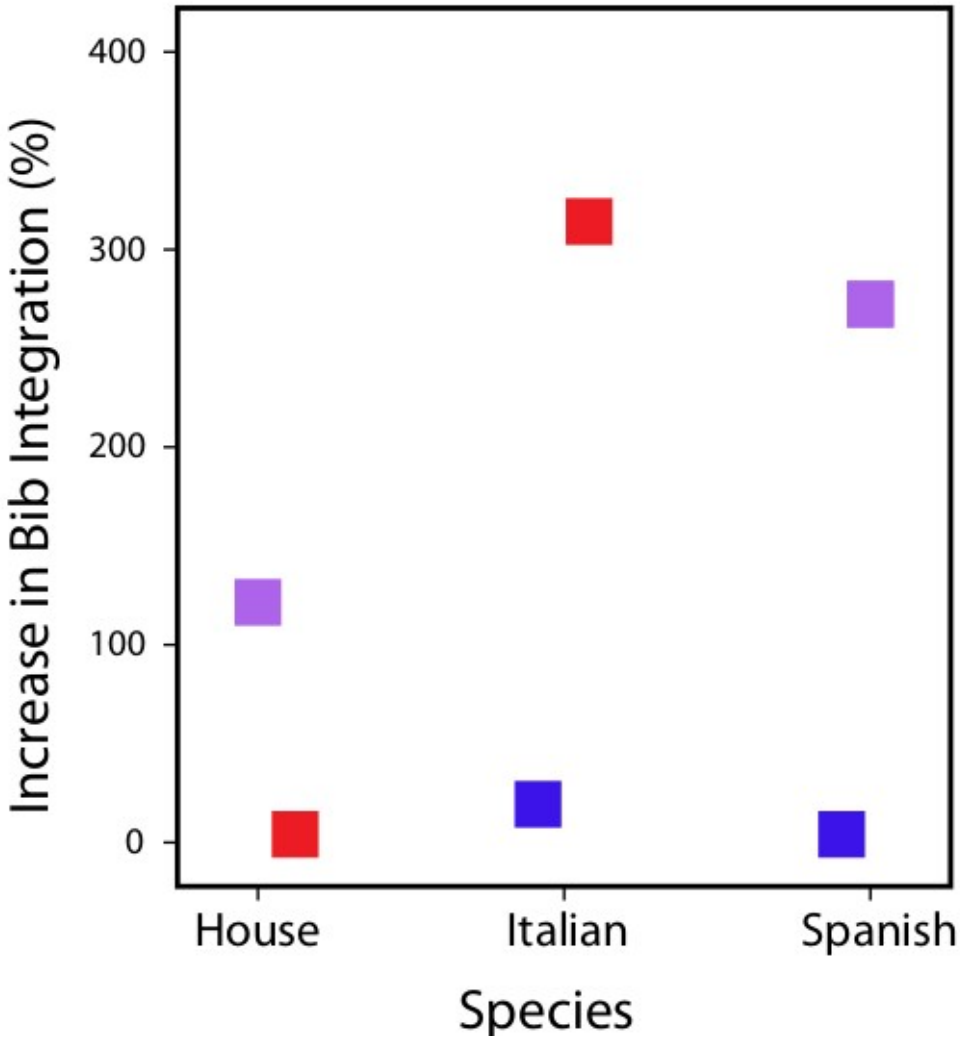


Figure 10. Percentage of increase of bib integration (based on the average absolute mean values of phenotypic correlation between the bib size and the other traits) from allopatry to sympatry across species. The colors refer to which species the species on the x-axis lives together with. Blue = house sparrow, violet = Italian sparrow and red = Spanish sparrow.



SUPPLEMENTARY

Table S1. Localities and detail information of samples

Country	Location	Geographic coordinates		Species	Ecology	Sample Size
		Latitude	Longitude			
Italy	Accettura (Basilicata)	40.49204	16.15893	Italian	Allopatric	30
Italy	Acquaviva	42.35164	13.94448	Italian	Allopatric	7
Italy	Assisi	43.07017	12.61752	Italian	Allopatric	9
Italy	Barletta	41.31928	16.28398	Italian	Allopatric	6
Italy	Burano (Toscana)	42.40	11.37853	Italian	Allopatric	5
Italy	Castel di Guido (Lazio)	41.90315	12.28384	Italian	Allopatric	6
Italy	Figline (Valdarno, Toscana)	43.62065	11.47031	Italian	Allopatric	2
Italy	Guglionesi (Molise)	41.91176	14.91644	Italian	Allopatric	14
Italy	Lago di Fondi (Lazio)	41.34419	13.35132	Italian	Allopatric	7
Italy	L'Aquila	42.35074	13.40	Italian	Allopatric	9
Italy	Lecce	40.35329	18.17401	Italian	Allopatric	6
Italy	Luni (Liguria)	44.06908	10.02219	Italian	Allopatric	6
Italy	Mantova	45.15952	10.80	Italian	Allopatric	1
Italy	Mass. Montanari (Gargano)	41.91303	15.84988	Italian	Allopatric	14
Italy	Mondolfo	43.75031	13.10	Italian	Allopatric	4
Italy	Ozzano D'Emilia	44.44357	11.47056	Italian	Allopatric	2
Italy	Rimini	44.06078	12.56626	Italian	Allopatric	13
Italy	Sanza (Campania)	40.24563	15.55361	Italian	Allopatric	11
Italy	Seisciano (Campania)	40.91704	14.48674	Italian	Allopatric	9
Italy	Staz. Populonia (Toscana)	43.00	10.5408	Italian	Allopatric	6
Italy	Terni	42.56022	12.64678	Italian	Allopatric	7

Italy	Ventotene (Lazio)	40.79346	13.42373	Italian	Allopatric	11
Italy	Aosta	45.73333	7.316667	Italian	Sympatric	5
Italy	Avigiliana	45.08333	7.40	Italian	Sympatric	10
Italy	Bardonecchia	45.83333	6.70	Italian	Sympatric	2
Italy	Bussoleno (I)	45.13333	7.15	Italian	Sympatric	1
Italy	Cormns	45.95	13.46667	Italian	Sympatric	1
Italy	L. Lesina (Gargano)	41.8605	15.3538	Italian	Sympatric	11
Italy	Oulx	45.03333	6.833333	Italian	Sympatric	4
Italy	Pont St. Martin	45.60	7.80	Italian	Sympatric	4
Italy	Pordenone	45.80	12.65	Italian	Sympatric	3
Italy	Saint Vincent	45.75	7.65	Italian	Sympatric	3
Italy	Saint-Rhmy-en-Bosses	45.83333	7.183333	Italian	Sympatric	2
Italy	Susa	45.13333	7.05	Italian	Sympatric	20
Italy	Valpelline	45.08333	7.333333	Italian	Sympatric	5
Slovenia	Ozeljan	45.94361	13.73028	Italian	Sympatric	1
France	Chambery	45.57	5.9118	House	Allopatric	9
Slovenia	Ljubljana	46.05139	14.50556	House	Allopatric	7
Slovenia	Postojna	45.78333	13.21667	House	Allopatric	3
Switzerland	Vouvry (CH)	46.33333	6.883333	House	Allopatric	1
Switzerland	Camping Sembrancher	46.08333	7.15	House	Sympatric	4
Switzerland	Liddes	45.98333	7.183333	House	Sympatric	3
Switzerland	St. Maurice	46.21667	7.00	House	Sympatric	5
Switzerland	Martigny	46.10	7.066667	House	Sympatric	7
Spain	Badajoz	38.65	7.216667	House	Sympatric	80
France	Modane	45.20	6.669167	House	Sympatric	2
France	St. Jean De Maurienne	45.27306	6.346111	House	Sympatric	6
Italy	Bardonecchia	45.83333	6.70	House	Sympatric	2
Italy	Manzano	45.98333	13.38333	House	Sympatric	1
Italy	Saint-Rhmy-en-Bosses	45.83333	7.183333	House	Sympatric	1

Italy	Pula	38.96843	8.976983	Spanish	Allopatric	16
Italy	San Priamo (Sardinia)	39.35884	9.560575	Spanish	Allopatric	23
Italy	Santa Margherita (Sardinia)	37.69278	13.02111	Spanish	Allopatric	9
Italy	Crotone (Calabria)	39.08074	17.12708	Spanish	Sympatric	2
Italy	L. Lesina (Gargano)	41.8605	15.3538	Spanish	Sympatric	12
Spain	Badajoz	38.65	7.216667	Spanish	Sympatric	36